AFRARCHAEA GRIMALDII, A NEW SPECIES OF ARCHAEIDAE (ARANEAE) IN CRETACEOUS BURMESE AMBER

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ABSTRACT. Afrarchaea grimaldii new species (Archaeidae, Archaeinae) from 88–95 Ma (Cenomanian–Turonian) Upper Cretaceous amber (Burmite) from Myanmar (Burma) is described. This is the first spider to be described from this deposit and is the oldest known Archaeidae sensu stricto extending the known range of the family by approximately 50 Ma from the previously oldest recorded specimens in Baltic and Bitterfeld ambers, and provides further evidence that spiders were not severely affected by the end-Cretaceous mass extinction event. It represents the oldest fossil record of an araneophagic spider. This species could be used to argue for both the theory of mobilistic biogeography and ousted relicts to explain the zoogeography of the genus, but until new data become available, supports neither reliably.

Keywords: Myanmar, fossil spiders

Biological inclusions have been known from Burmese amber or Burmite for almost a century (Cockerell 1916), but hitherto no spiders have been described from this source (Ross & York 2000). Some of the spider families present in the Burmese amber collections in the Department of Palaeontology of the Natural History Museum, London, were listed in Penney (2000) and Rasnitsyn & Ross (2000); (the specimens listed under the families Eusparassidae and Myrmeciidae by the latter authors (which are probably misidentifications, pers. obs.) are no longer valid arachnological taxa and should read Sparassidae and Corinnidae respectively [e.g. Platnick 2002]). Grimaldi et al. (2002) listed eleven families provisionally recorded from Burmese amber, including the specimen described here. Zherikhin & Ross (2000) proposed a Late Cretaceous age for Burmite, and based on the shared insect taxa of this amber with other well-dated amber deposits it probably dates from the Cenomanian or Turonian (Grimaldi et al. 2002). Cretaceous amber spiders have previously been described from the Santonian of Siberia (Eskov & Wunderlich 1994), the Turonian of New Jersey (Penney 2002), the Barremian of the Isle of Wight (Selden, 2002) and the Upper Neocomian-basal Lower Aptian of Lebanon (Penney & Selden 2002).

The Archaeidae are small to medium-sized haplogyne, ecribellate araneomorph spiders

which are distinguished from other spiders by the combination of promarginal cheliceral peg teeth and an abdomen-petiole stridulatory system (Forster & Platnick 1984). In addition, the three Recent genera: Afrarchaea Forster & Platnick 1984, Austrarchaea Forster & Platnick 1984 and Archaea Koch & Berendt 1854, have their carapace with the pars cephalica elevated above the pars thoracica, often constricted between the head (which bears long, slender chelicerae with a short fang) and thorax to form a distinct neck (Forster & Platnick 1984). Here, the first Cretaceous Archaeidae sensu stricto is described, from Burmese amber, and the systematics and biogeography of the family are briefly discussed. A checklist of fossil Archaeidae sensu lato is provided.

METHODS

Preservation.—Both specimens are preserved in Burmese amber or Burmite (for details of locality and stratigraphy, see Zherikhin & Ross 2000; Grimaldi et al. 2002) and belong to the Department of Entomology at the American Museum of Natural History (AMNH). The holotype, AMNH Bu-256 is preserved in a small piece (3 × 4 × 5 mm) of clear yellow amber suffused with darker bands, which represent layering of the resin at the time of exudation from the tree. This conclusion is supported because only one region, between two of these darker bands, contains

air bubbles. The spider is preserved in a layer without air bubbles; there are no syninclusions. There is some fracture damage as a result of specimen preparation however, overall this is an exquisitely preserved specimen.

Methods.—Prior to being received by the author the amber had been set in a clear plastic resin and cut and polished to reveal the inclusion. Further preparation was carried out at the AMNH as specified by the author to reveal further important taxonomic features. All measurements were made using an ocular graticule and are in mm. Drawings were done under incident light with camera lucidas attached to an Olympus SZH stereomicroscope and a Nikon Optiphot stereo compound microscope, and photographs were taken with a Nikon D1X digital camera attached to the Nikon microscope, using a 2.5× photoeyepiece and a 2× objective lens then manipulated in Adobe Photoshop.

Recent material examined.—Afrarchaea ngomensis Lotz 1996; 1 ♂, 1 ♀ from Ngome State Forest, KwaZulu/Natal Province; NCA 93/612 (coll. M. van der Merwe, Jan. 1993).

Abbreviations used in the text and figures.—In the leg formula (e.g. 1423), the legs are ranked in order of length (longest first). Tm is the ratio of the distance that a trichobothrium is located from the base of the metatarsus (e.g. Tm = 0.8 indicates that the trichobothrium is located eight-tenths of the way along the metatarsus, from the proximal end of the segment). Abbreviations used in the text and figures are as follows: ALE = anterior lateral eye(s); AME = anterior median eye(s); b = bulb; bs = blunt setae; car = carapace; cf = clypeal foramen; cs = cheliceral seta; e = embolus; ebl = extension of bulb lip; f = furrow; F = flaw in amber; fe = femur; fg = fang; LC = left chelicera; lot = lateral ocular tubercle; mt = metatarsus; mx = maxilla; op = opisthosoma; pa = patella; PLE = posterior lateral eye(s); PME = posterior median eye(s); Pp, = pedipalp; pt = peg teeth; RC = right chelicera; sp = spinneret region; T = trichobothrium; ta = tarsus; TA = tegular apophysis; ti = tibia; 1-4 = walking legs 1-4.

Repository abbreviations.—AMNH = American Museum of Natural History; AP = Amber Museum of Palanga, Lithuania; MCZ = Museum of Comparative Zoology, Harvard; MfN = Museum für Naturkunde Institut für Paläontologie, Humboldt-Universität zu Ber-

lin; NCA = National Collection of Arachnida, Plant Protection Research Institute, Pretoria; PIN = Palaeontological Institute of the USSR Academy of Sciences, Moscow; SGPIH = Geologisch-Paläontologisches Institut und Museum, Hamburg.

SYSTEMATIC PALEONTOLOGY

Family Archaeidae Koch & Berendt 1854 Subfamily Archaeinae Koch & Berendt 1854 *Afrarchaea* Forster & Platnick 1984

Type species.—Archaea godfreyi Hewitt 1919 by original designation.

Distribution.—Recent species in South Africa and Madagascar, fossil species in Burmese amber, Myanmar (Burma).

Remarks.—Afrarchaea was erected as a monotypic genus by Forster & Platnick (1984) for Archaea godfreyi from South Africa and Madagascar. It was distinguished from the other genera by having a less constricted carapace "neck" and on the basis of the female genitalia. Eskov (1992) considered Afrarchaea a junior synonym of Archaea; however, this was not based on the examination of Recent specimens and has not been accepted by subsequent workers (Platnick 2002). Lotz (1996) described five new Afrarchaea species from South Africa and provided new data for A. godfreyi.

Afrarchaea grimaldii new species Figs. 1-5

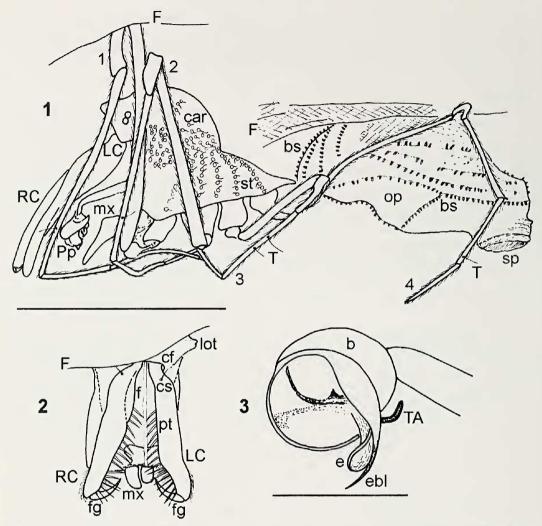
Archaeidae: Grimaldi et al. 2002: 28, fig. 18c.

Material examined.—Holotype: AMNH Bu-256, adult male, Burmese amber, Kachin: Tanai Village (on Ledo Road 105 km NW of Myitkyna); coll. Leeward Capitol Corporation 2000. Non-types: AMNH Bu-706, degraded specimen, same horizon and locality.

Diagnosis.—Afrarchaea grimaldii can be distinguished from all other species by having a bent tegular apophysis and a spoon-shaped embolus.

Etymology.—The specific epithet is a patronym in honor of Dr. David Grimaldi (AMNH) for his contributions to the study of amber and for loaning and assisting in the preparation of this material.

Description of holotype.—Body length 1.97; carapace 0.86 long, 0.43 wide, 0.64 high in region of pars cephalica; region between caput and thorax strongly developed and little differentiated from head; indent at junction



Figures 1–3.—*Afrarchaea grimaldii* new species. Holotype, AMNH Bu–256, Burmese Amber. 1, lateral view of whole specimen. 2, anterior view of chelicerae. Scale line 1.0 mm for both figures. 3, ventral view of pedipalp. Scale line 0.1 mm.

with pars thoracica 0.29 high, 0.46 long; with numerous distinct tubercles, each bearing a single seta lying flat against the carapace (Figs. 1, 5); narrow furrow running down midline from cheliceral foramen, visible when viewed anteriorly through the chelicerae (Fig. 2). ALE and PLE of equal size and contiguous, on a tubercle (Fig. 2), AME larger, PME not visible but presumably smallest as in Recent species (e.g. Lotz 1996). Clypeus slightly greater than diameter of AME. Chelicerae 0.79 long, slightly divergent and project out from the body at approximately 45 degrees when viewed laterally (Figs. 1, 5), strongly constricted basally where they insert into che-

liceral foramen, thickened in proximal half when viewed laterally and tapering slightly at their tips along fang furrow, lacking triangular projections on apical promargin; each has a single erect dorsal seta close to proximal constriction; lacking cheliceral dentition, but numerous peg-teeth along promargin and long strong hairs along promargin in fang region (Figs. 2, 4); lateral stridulatory ridges not visible but presumed to be present; fang short and curved backwards. Sternum 0.50 long, 0.16 wide, possibly tuberculate, lateral margins appear to project slightly between coxae. Labium longer than broad, maxillae considerably longer than broad, slightly convergent,



Figures 4–5.—Afrarchaea grimaldii new species. Holotype, AMNH Bu–256, Burmese Amber. 4, anterior view of chelicerae. 5, lateral view of whole specimen. Scale line 1.0 mm for both figures.

projecting from body at similar angle to chelicerae (Fig. 1). Opisthosoma 1.11 long, height and width uncertain, wrinkled surface (Figs. 1, 5), presumably a taphonomic artifact resulting from dehydration process associated with amber preservation, presumably subglobular in life; no dorsal scutum. Opisthosoma covered with small patches of chitinous tissue each of which bears short, fat, blunt seta; spinnerets and anal tubercle not clear and surrounded by chitinous ring (Figs. 1, 5).

Leg formula 1423; leg 1 fe 1.14, pa 0.29, ti 1.00, mt 0.49, ta 0.34, total 3.26; leg 2 fe 0.86, pa 0.19, ti 0.74, mt 0.36, ta 0.29, total 2.44; leg 3 fe 0.57, pa 0.19, ti 0.40, mt 0.29, ta 0.24, total 1.69; leg 4 fe 0.93, pa 0.19, ti 0.71, mt 0.40, ta 0.31, total 2.64. All leg segments without spines, but with pubescence of fine setae; each metatarsus with single trichobothrium (Tm 1-4 = 0.8-0.9); tibiae 1-3 with at least one dorsal trichobothrium, none visible on ti 4 (Fig. 1). Some leg segments show evidence of annulations and darker markings, particularly in distal region; three tarsal claws on onychium: paired claws toothed, unpaired claw simple. Pedipalp has relatively long femur, large rounded bulb, bent tegular apophysis and spoon-shaped embolus (Fig. 3).

Female.—Unknown.

Distribution and age.—Burmese amber, Myanmar (Burma); probably Upper Cretaceous (see Zherikhin & Ross 2000): Cenomanian—Turonian (see Grimaldi et al. 2002)

Remarks.—This specimen conforms with

the diagnostic characters of the genus given by Forster & Platnick (1984). It can be excluded from the remaining archaeid genera as follows: Archaea C.L. Koch & Berendt 1854. because it lacks the distinctive slender neck between the head region and the pars cephalica; Baltarchaea Eskov 1992, because it lacks the cephalic posterior angular projections, the abdomen does not extend beyond the spinnerets and the legs and chelicerae are not comparatively short; Mimetarchaea Eskov 1992, because it lacks the mimetid-like metatarsal spines on legs 1 and 2; Austrarchaea Forster & Platnick 1984, because the neck in the fossil specimen is too short, as is the embolus of the male palp; Jurarchaea Eskov 1987, because although Eskov (1987) was somewhat ambiguous with his diagnosis, in that he did not provide any distinct autapomorphies for his new taxa, but provided a list of general morphological descriptions that he later emphasized may be somewhat speculative, he placed this genus closer to the families Pararchaeidae and Holarchaeidae than Archaeidae sensu stricto. There are no spine-like horns sensu Lotz (1996) visible on pars cephalica of the fossil, but these are small in Recent specimens and may be present in the fossil but obscured by the legs or flaws in the amber. Specimen Bu-706 is preserved in a clear piece of amber with a spider syninclusion (possibly Oonopidae). It is severely degraded, barely visible, and it is only with a reasonable degree of imagination that the

raised pars cephalica and elongated chelicerae can be seen. For this reason it is very tentatively assigned to this species. Ecological observations of Recent archaeids are sparse, but all evidence suggests that they are araneophagic, free-moving, cryptozoic hunters (Forster & Platnick 1984). Most Afrarchaea in collections have been caught using pitfall traps or through sifting leaf litter (Lotz 1996). There is no evidence to suggest that the closely related families Holarchaeidae, Pararchaeidae and Mecysmaucheniidae are also araneophagous (Forster & Platnick 1984). Using the premise of behavioral fixity, which states that fossil organisms can be expected to have behaved in a similar manner to their Recent relatives at genus and often at family level, the specimen described above represents the oldest known occurrence of araneophagy in the spider fossil record (Jurarchaea belongs either in the family Pararchaeidae or Holarchaeidae [see Eskov 1987]). This is the first occurrence of Afrarchaea in the fossil record, taking the genus back 88-95 Ma, and is also the oldest record of the Archaeidae sensu stricto, extending the known range of this family by approximately 50 Ma from the previous oldest records in Baltic and Bitterfeld ambers. These fossils extend the known range of yet another Recent spider family through and beyond the end Cretaceous mass extinction event, suggesting that this catastrophe had little effect on the araneofauna, and provides further evidence for the great longevity for many Recent spider families (Selden & Penney 2001) and genera (e.g. Penney 2002).

DISCUSSION

The spider family Archaeidae is unique in that it was first described from three fossil species in Baltic amber (Koch & Berendt 1854) in a paper published posthumously by Menge (1854) who added three more new species. The first Recent species was discovered in Madagascar a quarter of a century later (O. Pickard-Cambridge 1881) and subsequently they have been found in Africa and other regions of the southern hemisphere (e.g. Harvey 2002). It is also, to my knowledge, the only family to have received paleontological treatment by that most eminent of arachnologists, Eugène Simon, who described a new species preserved in Baltic amber (Simon 1884). The specimens described by Koch & Berendt (1854) and Menge (1854) were considered lost for many years (e.g. Forster & Platnick 1984), however, many of Koch & Berendt's (1854) types are kept in the Institut für Paläontologie, Museum für Naturkunde, Zentralinstitut der Humboldt-Universität zu Berlin but those of Menge are still considered lost (Table 1).

The taxonomic composition and systematic

placement of the Archaeidae sensu lato con-

tinues to stimulate lively debate. Since its original description, ten Recent (two with fossil representatives) and four strictly fossil genera have at one time or another, been placed within the Archaeidae; these are now distributed among the six families: Archaeidae sensu stricto, Holarchaeidae, Mecysmaucheniidae, Pararchaeidae, Tetragnathidae and Salticidae (e.g. Eskov 1992; Platnick 2002). As currently delimited, Archaeidae sensu stricto contains 18 Recent species in three genera (Platnick 2002; Harvey 2002) and ten fossil species (Archaeidae sensu lato) in five genera (Table 1). Holl (1829) described the new genus and species Entomocephalus formicoides from Baltic amber. This was listed as belonging in the Archaeidae by Petrunkevitch (1958) and to my knowledge this is the only mention of this taxon in the literature since its description. Holl's figure of this specimen (plate 8: fig. 68a) is almost certainly a salticid probably belonging to the genus Myrmarachne Mac-Leay 1839, even though the figure and description have the specimen with only six eyes. If indeed this is the case, then under the ICZN law of priority, Entomocephalus Holl 1829, precedes Myrmarachne MacLeay 1839. However, the location of the specimen on which the description was based is unknown, and the description of the genus consisted of only one sentence. The name Myrmarachne is well established, in common usage and should probably be maintained unless Holl's fossil specimen can be located. Eoarchaea Forster & Platnick 1984 was erected based on a single immature amber spider (Forster & Platnick 1984). No mature specimens of this species are known and the fossils attributed to it probably belong to various other Archaea species (Eskov 1992).

Archaeidae was divided into four families: Archaeidae sensu stricto, Mecysmaucheniidae, Holarchaeidae and Pararchaeidae by Forster & Platnick (1984) in a review of the su-

was not found in their collections (Neumann pers. comm. 2002); § the type specimens of Menge (1854) are currently considered lost. His collection was Table 1.—Described fossil Archaeidae sensu lato (standard typeface = synonym). * = type species; † = fossil taxon; ? = dubious taxon; ‡ = the type specimens of Koch & Berendt (1854) were considered lost for many years but many are kept in MfN (Pietrzeniuk pers. comm. 1995), however, this specimen originally donated to the Westpreussische Provinzialmuseum, Gdańsk (formerly Danzig), which was established in 1880. In 1945 the collection was moved to a number of villages in northern Poland and has not been seen since. Although single samples of his collection have been found in Germany and Poland, there seems little hope that further items will be found (Koteja pers. comm. 2002; see Kosmowska-Ceranowicz [2001]).

Species	Type data	Distribution	Remarks
	AMNH Bu-256 SGPIH Type.Kat.Nr. 4351 Type lost§	Burmese amber Madagascan copal Baltic + Bitterfeld am-	Sub-fossil MCZ No. 7148 (129) designated
Archaea incompta Menge 1854	Tyrne locks	bers	as neotype (Petrunkevitch 1950)
Archaea levicata Koch & Recends 1864	Africats	Dailic amber	Considered a nomen nudum (Bonnet 1955)
Archaea paradoxa Koch & Berendt 1854* A. sphinx Menge 18548; Eskov 1992	Type lost;	Baltic amber Baltic amber	Non-type material: male, AP
			4092. Type species designation by Thorell (1870)
Archaea pougneti Simon 1884	Type female lost	Baltic amber	Two non-type males AP 14902, AP 6334 (o-Eo 17781/AP
Baltarchaea conica (Koch & Berendt 1854)* Archaea conica Koch & Berendt 1854	Type lost‡	Baltic amber	6334) Belongs to Mecysmancheniidae (Eskov 1992)
Jurarchaea zherikhini Eskov 1987*	PIN 2339/2607	Upper Jurassic, Ka-	Belongs in Pararchaeidae or Ho-
Mimetarchaea gintaras Eskov 1992*	AP 19566	Baltic amber	Belongs in Pararchaeidae or Ho-
			Jaichaeluae (ESKUV 1992)

perfamily Palpimanoidea. They also placed a number of disparate families (Mimetidae, Micropholcommatidae. Textricellidae) alongside the archaeoids, increasing the size of the Palpimanoidea considerably, which had previously consisted of only three families: Palpimanidae, Stenochilidae and Huttoniidae. However, few subsequent authors agreed with these authors' concept of the Palpimanoidea (see discussions in Eskov 1987, 1992; Coddington & Levi 1991), the monophyly of which was questioned. The superfamily Palpimanoidea was cut back to its original size by Schütt (2000), based on a reanalysis of the autapomorphies proposed by Forster & Platnick (1984). However, the correct systematic placement of the archaeids remains uncertain (Schütt 2000).

Fossils are often considered to be less useful than Recent specimens for systematic studies because of their imperfect preservation. However, they are of paramount importance in studies of historical biogeography, and can play a decisive part in the falsification of proposed hypotheses (e.g. Eskov 1990). For example, the current Gondwanan distribution of the Recent species of the spider family Archaeidae supports the theory of mobilistic biogeography i.e. that the fragmentation of Gondwanaland and the subsequent continental drift can explain their current distribution. However, because fossils of this family occur in Baltic amber (Koch & Berendt 1854) and from the Jurassic of Kazakhstan (Eskov 1987), the paleontological data contradict this hypothesis and a different explanation is required (the specimen reported from Dominican amber by Wunderlich [1999] is actually preserved in Madagascan copal [Wunderlich, pers. comm. 2000]). The theory of ousted relicts (e.g. Eskov & Golovatch 1986) proposes that austral disjunctions result from a formerly pancontinental distribution followed by the extinction of 'intermediate links' from the northern continents. There is a considerable amount of paleontological data, in the form of northern hemisphere fossil representatives of Recent austral taxa, which tends to be the rule rather than the exception, in support of this theory (Eskov 1987). This newly described amber archaeid spider provides new paleontological evidence that could be used to support both the above hypotheses. After a short phase of intra-continental rifting the breakup of east and west Gondwanaland was initiated by seafloor spreading between Africa and Madagascar in the Somali basin during the Jurassic quiet interval (c. 165 Ma), with the landmass of Madagascar + India eventually separating from Africa during the late Jurassic (152 Ma) (McLoughlin 2001). Madagascar separated from the Seychelles-India block 95-84 Ma and India migrated rapidly north reaching equatorial latitudes by the Eocene and combining with southern Asia (including West Burma) only about 43 Ma (McLoughlin 2001). West Burma had separated from northeastern Gondwana in the late Triassic-late Jurassic during the formation of the Neotethys Ocean and was accreted to southeast Asia by the late Cretaceous (McLoughlin 2001). Therefore, the occurrence of this genus in Burmese amber could be used to support the theory of mobilistic biogeography for its Recent distribution only if it existed throughout Gondwanaland during the late Triassic-late Jurassic. Three spiders have been described from the Triassic (Selden & Gall 1992; Selden et al. 1999) but none were placed in Recent genera. The currently more plausible explanation for the presence of Afrarchaea in this locality is that it is an ousted relict from a formerly pancontinental distribution in northern paleolattitudes as is the case for Archaea, another Recent archaeid genus, and presumably also the sister taxon of Afrarchaea.

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